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Sonderdruck aus „Zeitschrift für Tierpsychologie"

[Z. Tierpsychol., 24, 80—114, 1967]

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Verlag Paul Parey, Berlin u. Hamburg

Behavior of Elk *(Cervus canadensis)* during the Rut

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Behavior of Elk *(Cervus canadensis)* during the Rut

By Thomas T. Struhsaker*

With 22 figures

received 4. April 1966

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Introduction

The information relating to the behavior of elk *(Cervus canadensis)* is qualitatively incomplete and quantitatively undocumented. The primary purpose of this paper is to present more detailed descriptions of elk behavior observed during the rut and quantitative data on certain aspects of these behavior patterns. This does not represent a complete list of elk behavior. When possible, comparisons of my findings on elk behavior are made with those of other workers, in particular Altmann (1952, 1956, 1960), Graf (1955, 1956), and Murie (1932, 1951). Familial comparisons are not made, although some very good references on other cervids exist, e. g. Burckhardt, Cowan and Geist, Espmark, Geist, Lent and Pruitt.

Methods and Materials

This study was conducted in the Rocky Mountains of Banff National Park, Alberta, Canada. The majority of observations were made in the Cascade Valley (115° 45' W., 51° 30' N.) between 26 August and 26 October 1965. The elevation in the main study area ranged from 5,400 feet to 10,000 feet. In addition, elk were photographed, taperecorded, and observed for three days in the Kootenay National Park, British Columbia located about 40 miles southwest of the main study area. A general survey of the main study area was made between 16 and 19 August.

A total of 115 hours of direct observation were made on elk. This includes only those times when the elk were undisturbed by my presence and when I was systematically taking notes. In addition, many hours were spent photographing, taping, and stalking. The elk were relatively shy in this region and an observer had to stalk and remain hidden from them. Observations were made at distances of about 30 feet to three-quarters of a mile. Two pairs of binoculars were used, a 20×60 Bushnell mounted on a tripod and a 7×35 Tower. Photographs were taken with a 35 mm Exakta, a 400 mm Novoflex, and a 50 mm Zeiss lens. Tape-recordings were made with a Nagra tape-recorder at $7^1/_2$ ips and an

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Electro-voice microphone. The tape-recordings were analyzed using the high shaping switch and the wide band-pass filter of a Kay Electric Sona-graph.

Important terms used throughout this paper are defined as follows. The *rut* of a species is understood to be the periodically recurring sexual arousal of that species. The term rut is apparently derived from the Latin word rugitus meaning "a roaring". It is usually inferred that copulation with insemination accompanies this sexual arousal. In this study, complete heterosexual mounting was seen only five times and it was never determined if insemination occurred. It is assumed that the other patterns of heterosexual behavior are an adequate indication of sexual arousal and copulatory behavior. Ideally, the peak of the rut should be referred to as the time when the greatest amount of insemination occurs. However, in the absence of such information, the peak of the rut will be referred to as the time when heterosexual activity is at its highest. As seen in the section on heterosexual behavior, the peak of the rut during this study occurred between 8 and 21 September.

The elk were divided into six age-sex classes: calves, cows, spikes ($1^1/_2$ year old males), $2^1/_2$ year old bulls, $3^1/_2$ year old bulls, and bulls older than $3^1/_2$ years. Calves were readily distinguishable as being the smallest individuals in the population. All individuals without antlers and larger than the calf class were considered as cows. The distinction of the male classes (spikes and older bulls) was based upon the criteria given by Murie (1951), namely antler size and shape, and number of antler points. On some occasions, I had difficulty categorizing bulls as being $3^1/_2$ years or older than $3^1/_2$ years. My tendency in such cases was to categorize them as being older than 3½ years. This difficulty migth account, at least in part, for the relative paucity of data for $3^1/_2$ year old bulls evident in several parts of this paper.

Social Structure

The social structure of elk, as observed during this study period, seemed to be extremely complex, due largely to the fact that they lived in a relatively dynamic society in which individuals apparently moved quite frequently from one group to another. The situation was further complicated by a seasonal change in the size and composition of groups. Certain associations such as the cow-calf relationship are probably quite stable. In addition, cows of the same age class may form relatively stable associations. But even the cow groups appeared to be dynamic. Cows with calves were seen joining cow groups and cow groups were observed to be divided by competing bulls.

Groups or associations of many types were seen, including groups with adults of both sexes and groups with adults of only one sex. In addition, solitary individuals were commonly seen. The permanence of these associations or groups was not determined. However, the size and composition of all groups or associations encountered were recorded. These associations have been divided into three categories: cow groups, bull groups, and solitaries. The category of cow groups includes *harems*. Harems developed during the rut and were characterized by the association of several cows and calves with one adult bull. This bull defended the association against the approach of other bulls.

The data on the size and composition of cow groups are summarized in Tab. 1. Although the data for several of the time-periods are too few to permit statistical treatment, certain tendencies are suggested. Apparently, the size of cow groups decreased with the onset of the rut and then increased with the waning of the rut. The percentage of cows and calves in the groups remained relatively stable. The percentage of spikes, $2^1/_2$, and $3^1/_2$ year old bulls decreased as the rut progressed and increased as the rut waned. These data also indicate that the spikes remained in the cow groups longer and rejoined them sooner than did the $2^1/_2$ and $3^1/_2$ year old bulls (see also Figs. 1 and 2). It is further seen from these data that prior to the rut no bulls older than $3^1/_2$ years were in the groups, whereas with the onset of the rut the percentage of such bulls in cow groups remained quite constant.

Tab. 1: Size and Composition of Cow Groups

Date	No. groups counted	Range, mean, and percentage of:						
		Cows	Calves	Spikes	$2^1/_2$ yr. bulls	$3^1/_2$ yr. bulls	$>3^1/_2$ yr. bulls	Total group size
16 – 19 Aug	4	5 – 57 21.25 60.71 %	3 – 23 10 28.57 %	0 – 6 2 5.71 %	0 – 2 1 2.85 %	0 – 2 0.75 2.14 %	0 0	8 – 90 35
25 – 31 Aug	5	4 – 15 9.2 65.71 %	2 – 4 2.6 18.57 %	0 – 3 1 7.14 %	0 – 1 0.20 1.42 %	0 0	1 1 7.14 %	7 – 21 14
1 – 7 Sept	6	3 – 10 5.83 58.3 %	1 – 4 2.83 28.3 %	0 – 3 0.50 5.0 %	0 0	0 0	0 – 1 0.83 8.3 %	5 – 14 10
8 – 14 Sept	4	1 – 11 5 58.8 %	0 – 4 2 23.5 %	0 – 1 0.50 5.8 %	0	0	1 11.76 %	2 – 17 8.5
15 – 21 Sept	7	3 – 19 11.57 68.62 %	1 – 6 4.00 23.72 %	0 – 2 0.29 1.72 %	0	0	1 5.93 %	7 – 26 16.86
22 – 28 Sept	13	1 – 18 6.62 64.20 %	1 – 11 2.62 25.41 %	0 – 2 0.23 2.23 %	0	0	0 – 1 0.77 7.46 %	3 – 31 10.31
29 Sept – 5 Oct	11	1 – 8 3.27 58.91 %	0 – 3 1.64 29.54 %	0 – 1 0.09 1.62 %	0	0	0 – 1 0.55 9.90 %	2 – 12 5.55
6 – 12 Oct	3	4 – 21 11.33 69.38 %	2 – 4 2.67 16.35 %	0 – 4 1.33 8.14 %	0	0	1 6.12 %	7 – 30 16.33
13 – 19 Oct	11	4 – 23 12.29 67.19 %*	2 – 11 4.71 25.75 %*	0 – 3 0.64 0 – 1 0.29 1.58 %*	0 – 1 0.18 0*	0	0 – 1 0.91 1 5.46 %*	7 – 45 24.27 7 – 28 18.29*
20 – 26 Oct	6	3 – 21 11.33 60.16 %	2 – 11 2.64 14.02 %	0 – 3 1.33 7.06 %	0 – 1 0.33 1.75 %	0	0 – 1 0.83 4.40 %	6 – 36 18.83

* Based on 7 groups only due to inadequate counting of other four groups.

Fig. 1 presents additional information on the composition of cow groups. Prior and subsequent to the peak of the rut cow groups without bulls or spikes were seen. However, during the most intense period of the rut (8—21 September, see below) all cow groups had bulls and/or spikes with them. In addition, it is seen that all cow groups had a bull older than $3^1/_2$ years with them during the peak of the rut.

Tab. 2 summarizes the data on size and composition of bull groups. A most obvious change occurred in the composition of the bull groups. Prior to the rut the bull groups were composed exclusively of bulls older than $3^1/_2$ years. With the onset of the rut the bull groups were primarily composed of spikes and young bulls. In addition, it seems apparent that the largest bull groups were developed during the peak of the rut (8—21 September).

Fig. 2 presents further information on the seasonal changes of the distribution of the spikes and bulls among the society. Several trends emerge from these data. Prior to the rut the majority of bulls older than $3^1/_2$ years occurred in bull groups, whereas virtually all of the spikes and $2^1/_2$ year old bulls and

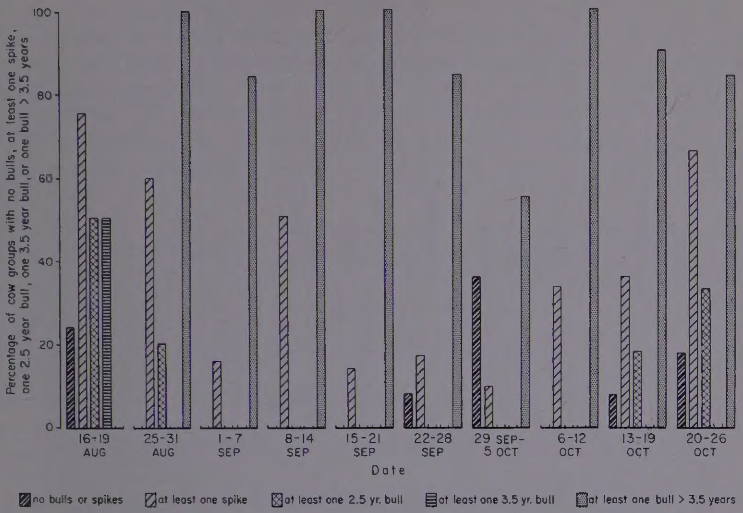


Fig. 1: Seasonal changes in male-composition of cow groups

Tab. 2: Size and Composition of Bull Groups

Date	No. groups counted	Range, mean, and percentage of :				
		Spikes	2½ yr. bulls	3½ yr. bulls	>3½ yr. bulls	Total group size
16 - 19 Aug	4	0	0	0	2 - 4 3 100 %	2 - 4 3
25 - 31 Aug	2	0	0	0	2 2 100 %	2 2
1 - 7 Sept	No bull groups counted					
8 - 14 Sept	2	2 2 100 %	0	0	0	2 2
15 - 21 Sept	2	1 - 3 2 20 %	2 - 8 5 50 %	1 - 3 2 20 %	0 - 2 1 10 %	8 - 12 10
22 - 28 Sept	7	0 - 4 1.71 37.41 %	0 - 5 2.29 50.10 %	0 - 2 0.43 9.40 %	0 - 1 0.14 3.06 %	2 - 9 4.57
29 Sept - 5 Oct	6	0 - 5 1.67 45.50 %	0 - 4 1.33 36.23 %	0 - 3 0.50 13.62 %	0 - 1 0.17 4.63 %	2 - 6 3.67
6 - 12 Oct	1	0	2 100 %	0	0	2
13 - 19 Oct	3	0 - 2 0.67 15.47 %	0 - 6 2 46.18 %	0 - 2 0.67 15.47 %	0 - 2 1 23.09 %	2 - 8 4.33
20 - 26 Oct	1	2 40 %	3 60 %	0	0	5

many of the $3^{1}/_{2}$ year old bulls occurred in cow groups. Coincident with the rut the majority of bulls older than $3^{1}/_{2}$ years occurred in cow groups as harem bulls or were solitary. The data for $3^{1}/_{2}$ year old bulls are sparse, but indicate that the majority of such bulls were solitary or in bull groups during the rut. Most of the $2^{1}/_{2}$ year old bulls and spikes spent the rut in bull groups, which commonly remained on the periphery of harems. Fig. 2 also substantiates the conclusion that the spikes remained in the cow groups longer and rejoined them sooner than did the $2^{1}/_{2}$ and $3^{1}/_{2}$ year old bulls.

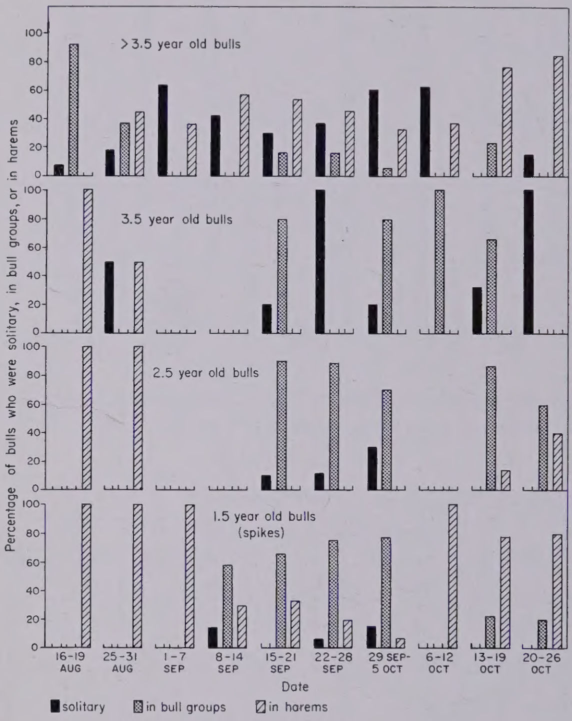


Fig. 2: Seasonal changes in the distribution of males in the society

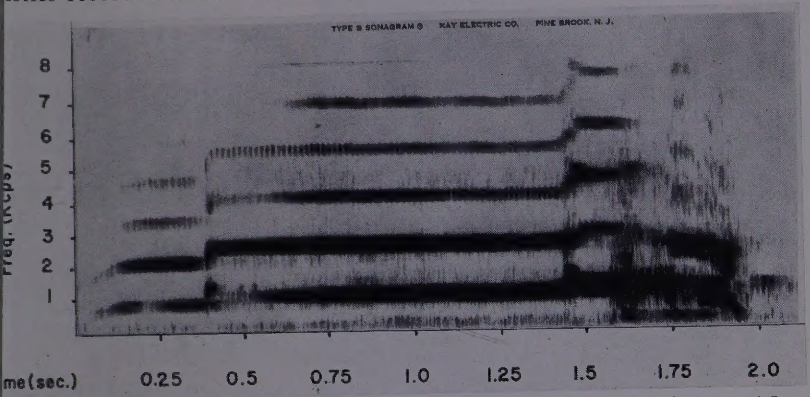
The foregoing conclusions are probably best explained in the following manner. Prior to the rut the bulls older than $3^{1}/_{2}$ years remained outside of the cow groups. With the onset of the rut these older bulls became sexually aroused and more aggressive toward other bulls. Such behavioral changes resulted in these older bulls entering the cow groups, splitting the cow groups into smaller groups through competition with other old bulls, and driving the spikes and younger bulls out of the cow groups. The spikes and younger bulls then formed bull groups. The occurrence of large bull groups during the peak of the rut might have been due to the convergence of several smaller bull groups and solitary bulls upon a harem (cow groups). As the rut began to wane, the spikes and eventually the younger bulls rejoined the cow groups, presumably, as the tolerance of the harem bulls for the young males increased. A decrease in the sexual arousal and aggressiveness of the older bulls may be responsible for the reformation of large cow groups which was apparently occurring at the time this study was terminated.

Rutting Behavior

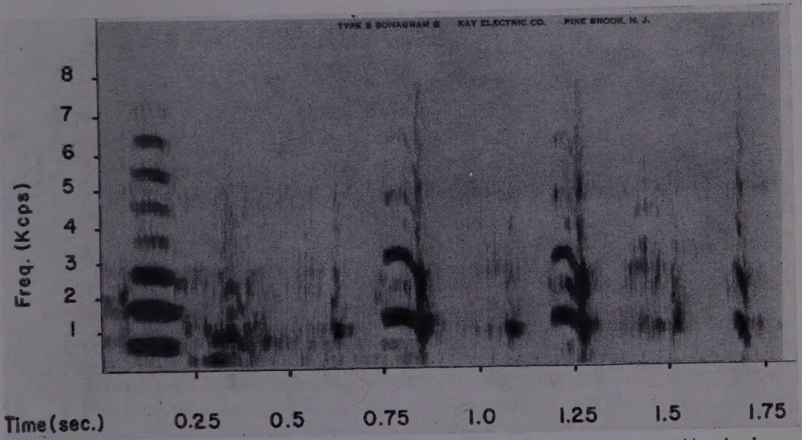
The behavior patterns described in this section were directly or indirectly related to sexual behavior and occurred primarily or exclusively during the rutting season.

a) Whistling

The whistling of elk bulls is also commonly referred to as bugling. This alization has been rather well described by MURIE (1932), who emphasized variability. Generally there was a high-pitched portion of relatively high plitude. The high-pitched portion was commonly terminated with a moan bellow of apparently lower amplitude, or with a series of yelps or yips. ese terminal vocalizations sometimes occurred alone. Sonagrams of some istles recorded under field conditions are presented in Figs. 3 and 4. It is



. *3:* Whistle given by a bull older than 3$^{1}/_{2}$ years (note moan portion between 1.5 and) seconds)



ig. 4: Four yelps given by a bull older than 3$^{1}/_{2}$ years (ignore echoes and/or background oise at 0.38, 0.62, 1.12, and 1.50 seconds)

een in Fig. 3 that the high pitched portion of whistling was a well-structured, onal sound with a fundamental at about one kilocycle per second (Kcps) and with two to four high-energy overtones. The moan portion (Fig. 3) was a non-onal sound with the majority of its energy being between 0.080 (base line) nd 2 Kcps. The duration of a complete whistle ranged from 2.50 to 2.85 econds. Yelps are tonal sounds with a fundamental between about 0.8 and .5 Kcps and the development of two to six overtones (Fig. 4). Yelps ranged n duration from 0.05 to 0.25 seconds.

While whistling, a bull's head was level with or slightly below his shoulders, his muzzle was held horizontally, and his head appeared to be extended. His mouth was open, but his lips were not retracted. Sometimes the mouth was puckered into an "O" shape. The bull's ears were tilted or laid back against his head and neck with their orifices facing outward (Fig. 5). While yelping, the ventral and ventro-lateral abdominal area immediately anterior to the hindlegs of the bull pumped in and out. On some occasions the bull's penial region palpitated as he whistled. Sometimes this palpitation was accompanied by an erection of his penis and the expulsion of a clearcolored fluid in spurts from the penis.*)

Only bulls that were $2^1/_2$ years old or older were heard to whistle. The $2^1/_2$ year old bulls seemed to have a whistle of higher pitch than the older bulls.

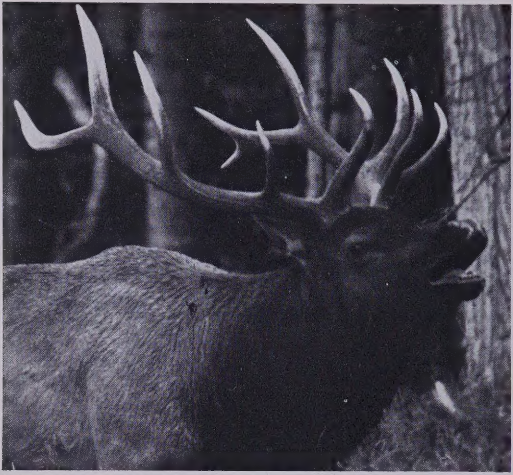


Fig. 5: A bull older than $3^1/_2$ years whistling

Whistling occurred under a wide variety of circumstances. Bulls commonly whistled after cows that they had approached moved away from them; after herding cows and calves;after a complete sexual mount of a cow; after thrashing saplings or shrubs; after and before digging the ground with their antlers; while completely alone; while recumbent; by members of all-bull groups; and by bulls peripheral to a harem. Yelping was sometimes given as a bull approached a cow.

Whistling was heard at all times of the day. On the night of the 10th and 11th of September 1965, I recorded at half hour intervals the number of whistles heard within a five minute period. This sampling was begun at 1900 hours on the 10th and terminated at 0730 hours on the 11th. Throughout is sampling I remained in one place. Whistling occurred throughout the ght. The number of whistles heard in a five minute period ranged from to 39. However, this sampling method fails to account for the possibility at bulls moved into and/or out of the area of audibility during the night.

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*) The emission of a clear-colored fluid in spurts from the penis occurred in a variety of circumstances (see below). This emission was always accompanied by palpitation of the penial region and sometimes by an erection of the penis, which jerked back and forth along the sagittal plane. Only bulls that were estimated to be $3^1/_2$ years or older were observed to emit this clear fluid. On only one occasion out of 28 cases was the fluid yellow. Female elk were observed to emit a yellow fluid (urine presumably) in a steady stream or in spurts from their perineal region. On at least one occasion a female elk emitted a clear fluid in spurts from her perineal region. In addition, a five-point bull, who was estimated to be about $3^1/_2$ years old, was twice seen to pass a yellow-colored fluid (presumably urine) in a steady stream that flowed downward vertically from his penis. No palpitation of the penial region nor erection of the penis accompanied this flow. The bull stood in a "normal" posture and fed as he passed this fluid. Thus, although the identity of the clear-colored fluid emitted in spurts by bulls was not determined and several possibilities exist, it seems quite likely that it was ejaculate, which, on at least one occasion, was mixed with yellow-colored urine. However, GRAF (1955) was of the opinion that this fluid was urine. Hereafter, this phenomenon will be referred to as ejaculation. If in fact this fluid was ejaculate, it seems that from an evolutionary viewpoint ejaculation in vacuo would be non-adaptive unless it had assumed an additional function secondary to insemination. It is suggested later in this paper that ejaculation in vacuo may have functioned as a system of olfactory marking.

Additional quantitative data on whistling were obtained by individual mpling (see below). These data are summarized in Tab. 3: fewer whistles ccurred at midday (1100—1300 hours) than early (0700—0900 hours) or te (1700—1900 hours) in the day. Furthermore, these data suggest that olitary bulls whistled more than harem bulls. The first finding is, apparently, reflection of the diurnal periodicity of behavior, additional examples of hich are considered below. The second finding, if significant, is not under- ood.

b. 3: Whistle-frequency (number whistles/minute) as related to time of day and social affiliation

	Time of day		
	0700 - 0900	1100 - 1300	1700 - 1900
> 3.5 yr. harem bull	0.47	0.27	0.50
> 3.5 yr. solitary bull	0.70	0.28	0.94

The function and significance of whistling is not clear. No overt response y cows or calves to whistling was apparent. On some occasions bulls were bserved exchanging several whistles and approaching one another. Further- ore, I demonstrated to myself a phenomenon that is well known to hunters nd elk-watcher. One can call bull elk to oneself by imitating the whistle. ometimes even an exceedingly poor imitation is capable of evoking whistles rom a bull, and eventually his approach after several exchanges of whistles. This may apply only to solitary bulls. It is tentatively suggested that the vhistling of bull elk communicates to other elk the existence and location of a exually mature and sexually receptive bull. The response of other bull elk s to whistle and approach the other whistling bull when the latter is not earby or visible. The adaptiveness of such an attraction lies in the nature nd outcome of the resulting encounter. For example, if a solitary bull was ttracted to a bull in possession of a harem and a sparring encounter resulted, he stronger bull would, presumably, take possession of the harem and copu- ate with the cows. This would be selected for through differential reproduc- ive success. Alternatively, the harem might be split by these two bulls, each taking possession of a portion of the original harem. This alternative would lso be adaptive in that it would undoubtedly increase the genetic variability of the population. The mutual attraction of two solitary bulls would be adaptive if such an attraction led to a sparring encounter, which might in turn lead to the establishment of a dominance relationship between these two bulls. Such a dominance relationship would affect the future encounters between these two bulls. This would be of differential reproductive significance when one of these bulls was in possession of a harem.

b) Thrashing and Digging with Antlers

During the rut, male elk used their antlers to thrash shrubs and coniferous saplings. The brow and bay tines were used most extensively. During thrashing, the ears, muzzle, and neck were rubbed extensively, the head being moved back and forth and up and down with varying intensities. The position of the bull's head was largely determined by the level of the vegetation being thrashed. Thrashing was performed from a standing or recumbent position. A bull sometimes closed his eyes partially or completely as he moved his face downward through the vegetation. The saplings thrashed in this manner were denuded of many branches and much of their bark. Newly thrashed saplings were extremely conspicuous because of the exposure of their light-colored wood. Recently thrashed saplings looked different from saplings that had been thrashed at an earlier time as a result of darkening of the exposed wood. The longest bout of trashing observed, performed by a large, six-point bull in possession of a harem, lasted eight minutes and fifteen seconds.

In addition, bull elk used their antlers, especially the brow and bay tines, to dig dirt, moving the head up and down and back and forth. Commonly intermingled with this digging was a pawing of the ground. One forefoot was extended forward and then brought down and back rapidly. This action was repeated several times in rapid succession. Particular locations were frequently pawed and dug on more than one occasion and quite likely by more than one bull. Such areas were visually conspicuous. After working the ground in this manner, a bull commonly laid down in the freshly worked dirt. While recumbent in this dirt a bull sometimes rubbed the sides of his face on the ground. Some of the waxy and odiferous secretion of the preorbital glands might have been rubbed into the dirt.

Thrashing and digging were commonly intermingled with muzzling of the ground, in which a bull placed his muzzle near or in contact with the ground for several seconds, probably for the purpose of smelling. Subsequent to muzzling the ground, the penial region of the bull palpitated and/or the penis became erect and was jerked back and forth along the sagittal plane.

In a typical sequence a bull dug the ground with his brow and bay tines and occasionally pawed the ground with a forefoot. Intermittently, he muzzled the ground. Throughout the sequence his penial region palpitated. While standing motionless or while digging he ejaculated. The ejaculate shot forward in spurts landing on the freshly worked dirt, his forelegs, and throat (see Graf 1955). The bull then lay in the area that had been worked.

Bulls that were $1^1/_2$ years or older and rarely spikes in velvet were seen to thrash vegetation with their antlers. Furthermore, certain aspects of the pattern were not seen in males $2^1/_2$ years or younger, including palpitation of the penial region, penial erection, and ejaculation. Only bulls that were $2^1/_2$ years or older were observed to dig and paw the ground.

Thrashing and digging were performed by bulls that were solitary, in bull groups, on the periphery of harems, or in possession of harems.

No overt response by other elk to the thrashing or digging of a bull was seen.

Freshly thrashed vegetation and, especially, areas that had been freshly dug and pawed sometimes had a musky odor*) that was very conspicuous to the author. Although Graf (1955) did not detect any such scent about freshly worked saplings, he did feel that such saplings were a means of marking. It seems reasonable to assume that thrashing and digging communicate the location and temporal proximity of sexually mature and sexually receptive bull elk to other bull elk. As with whistling, this system of marking may attract bulls to one another (see above).

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*) This odor might have been from the "ejaculate" and/or preorbital gland secretions.

c) Wallowing

Wallowing during the rut was performed only by males $1^{1}/_{2}$ years or r. Wallows were found primarily in boggy areas and consist, in essence, of ol of viscous mud (see MURIE 1951). Many of the wallows had obviously used several times and, undoubtedly, by more than one bull. While lying wallow a bull would typically rub his neck, throat, muzzle, antlers, and ides of his face on the edge of the wallow. The edges of wallows were rmer composition than the damper central portions. It is conceivable that bull rubbed the sides of his face on the edges of a wallow he was also ing some of the secretion of the preorbital glands into the soil. On one sion a bull ejaculated while standing in a wallow. Possibly related to this e fact that freshly used wallows had a distinct musky odor (see GRAF 5). Bulls laid in wallows for hours on end, but the actual rubbing lasted a few seconds.

Only once did a male elk roll about in a wallow. On this occasion a spike h velvet lay in a wallow and rocked back and forth laterally and thus ed his entire ventral surface in the mud. He performed this rocking twice, etween which he gamboled, turned in circles, trotted in an alert manner, stotted (see below) near the wallow. After the second rubbing in the low the spike stotted away from the wallow and was followed by another e (who was out of velvet) and a $1^{1}/_{2}$ year old cow, both of whom also ted. MURIE (1951) did not observe spike bulls wallowing.

Wallowing was performed by bulls that were solitary, in bull groups, the periphery of harems, or in possession of harems. The immediate stimu- evoking wallowing was not apparent. In addition, no overt response by er elk to the wallowing of a bull was discernible.

During the rut, many bulls were seen with dried mud on their sides and tral surface. Presumably, this mud was derived from wallowing. The pre- ce of dried mud on a bull made him visually conspicuous and distinctive m other elk at a relatively great distance.

It is tentatively suggested that the function of wallowing is to facilitate location of bulls by one another. This facilitation would be accomplished the olfactory and visual stimuli of the actual wallow and by the visual nulus of the mud-covered bull. As with whistling, thrashing, and digging, adaptiveness of such attraction may lie in the resulting sparring encounters their facilitation of differential reproduction (see *Whistling* above).

d) Sparring

Under the category of sparring are included encounters between two tlered males in which they faced one another with heads lowered, antlers contact, and in which they pushed and clashed their antlers (Fig. 6).

Sparring encounters among bulls that were $2^{1}/_{2}$ years or younger were re gentle and usually briefer than among older bulls. Among the younger lls ($< 2^{1}/_{2}$ years) sparring encounters were usually, if not invariably, eceded by one or both of two gestures; head bobbing and presenting antlers. the head bobbing gesture one bull faced another and bobbed his head up d down along the sagittal plane several times in succession. Sometimes both lls bobbed their heads toward one another simultaneously. While bobbing s head, the bull's muzzle never rose above the horizontal plane (upward rtion of bob) and seldom beyond the vertical plane (downward portion of b). Thus the muzzle of the displayer moved through a relatively small arc.

However, on some occasions the bob was greatly exaggerated such that the bull's muzzle nearly touched the ground. Sometimes a bull gave only one bob and then held his head in the lowered position, moved toward his opponent, and began sparring. While head bobbing the bull's legs were not flexed nor were his ears noticeably deflected from the "normal" upright position. Apparently, head bobbing represented an incipient lunge and functioned as a threat gesture (see Murie 1951).

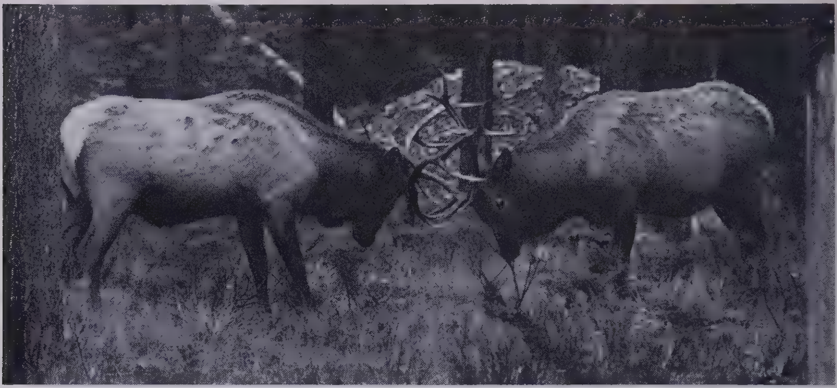


Fig. 6: Two young bulls in a typical sparring encounter

In the presenting antlers gesture, a bull lowered his head such that his muzzle nearly touched the ground. He then rotated his head on its longitudinal axis such that his antlers were directed toward his opponent. Concomitantly his muzzle was directed away from his opponent. This gesture might also be termed an antler display. It undoubtedly functioned as a threat gesture.

Subsequent to either of these gestures the younger bulls ($< 2^1/_2$ years) slowly lowered their muzzles near the ground and then gently touched the tips of their antlers together, whereupon sparring ensued.

During the actual sparring a bull laid his ears back against his head and neck. In addition, on the few occasions when I was relatively close to bulls that were sparring I heard a squealing-like call that greatly resembled the cohesion squeal (see below). This call might be written as nyeah, eeyow, nyeow, or yeow. This call was heard only from bulls that were $2^1/_2$ years old.

The most intense sparring encounters occurred between bulls that were $3^1/_2$ years or older. This was especially so when one of the combatants was in possession of a harem. Such sparring was never preceded by the gesture of presenting antlers and only occasionally by head bobbing. In spite of the greater intensity of these encounters the occurrence of a body blow was observed only once in a total of 49 sparring encounters observed in detail. On this occasion two large, six-point bulls were sparring. One was in possession of a harem and the other was challenging him. As the bulls sparred one of them fell or was knocked onto his side. His opponent immediately rushed in and landed a body blow with his antlers. Subsequently, the recipient of this blow had a long scrape along the entire length of his left side. No blood was seen. He immediately rose to his feet and the sparring was resumed. Eventually, the harem was split up between these two bulls. Although intense parring encounters in which body wounds are inflicted or one of the partiipants is killed do occur (GRAF 1955), it is the impression of this author and MURIE (1951) that such encounters are extremely rare and play a very minor ole in the population dynamics of elk.

Sparring encounters were terminated in several ways. Among the younger bulls (< $2^1/_2$ years) and in less intense encounters the termination was most variable. The two participants sometimes appeared to cease sparring simulaneously. On other occasions the two participants walked or trotted parallel o one another bobbing their heads towards one another. In an additional variation, one of the participants gamboled (see below) away from the other (see ALTMANN 1952). This latter pattern occurred only among bulls $2^1/_2$ years old or younger.

Among the older bulls and in the more intense encounters the sparring was commonly terminated as one of the participants turned and trotted or galloped away.

Sparring was engaged in by antlered males of all ages who were out of velvet. It occurred within bull groups, among bulls peripheral to a harem, and between a bull in possession of a harem and peripheral or challenging bulls.

When a harem was surrounded by two or more peripheral bulls it was common to observe the bull in possession of a harem running back and forth between his harem and the peripheral bulls, sparring with and chasing the bulls and herding the cows and calves. While the harem bull sparred with one of the peripheral bulls, other peripheral bulls commonly ran into the midst of his harem and approached and herded cows and calves. In such cases the harem bull would cease sparring and chase the intruders. Sometimes while chasing other bulls, the harem bull assumed a posture in which his head was lowered to the level of his shoulders and his muzzle held horizontal. This posture was maintained as he trotted or galloped after a peripheral bull. This posture seemed to be displayed only when the distance between the chaser and chasee was relatively short (about 25 yards or less). In addition, this pattern was very similar, if not identical, to the extended head threat or herding posture (see below).

(I) Quantitative data on combatants

The data on sparring encounters are summarized in Tab. 4. Although a total of 49 encounters were observed, only 45 are considered in this table due to the fact that in four of them the age-class of one or both participants were not determined. These data are presented as: number of encounters per bull-pair-minute. A bull-pair-minute is the product of the number of pair-combinations of the particular age-class(es) considered in the group observed

Tab. 4: Sparring Encounters

Same age-class	No. encounters / bull-pair-min.	Different age-class	No. encounters / bull-pair-min.
S vs S	0.00052	S vs $2^1/_2$	0.00020
$2^1/_2$ vs $2^1/_2$	0.0030	S vs $3^1/_2$	0
$3^1/_2$ vs $3^1/_2$	0.013	S vs $>3^1/_2$	0
$>3^1/_2$ vs $>3^1/_2$	0.064	$2^1/_2$ vs $3^1/_2$	0.00068
		$2^1/_2$ vs $>3^1/_2$	0
		$3^1/_2$ vs $>3^1/_2$	0

S = spike, $2^1/_2$ = $2^1/_2$ year bull, $3^1/_2$ = $3^1/_2$ year bull, $>3^1/_2$ = $>3^1/_2$ year bull and the number of minutes spent observing the group with this number of pair-combinations. This product corrects for differences in observation time and differences in group size and composition. For example, consider the hypothetical case in which we observe a group of four spikes and two $2^1/_2$ year old bulls for thirty minutes. There are six possible spike-spike pairs, eight possible spike-$2^1/_2$ year bull pairs, and one possible $2^1/_2$-$2^1/_2$ year bull pair. The number of bull-pair-minutes for each of these three pairings is the number of possible pairs times the number of minutes of observation, *i. e.*, spike-spike: $6 \times 30 = 180$; spike-$2^1/_2$ year: $8 \times 30 = 240$; and $2^1/_2$-$2^1/_2$ year: $1 \times 30 = 30$.

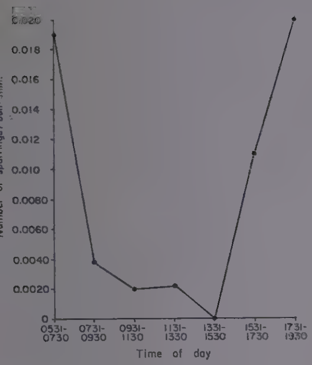
The data in Tab. 4 have been segregated into columns based on whether the combatants were of the same age-class or of different age-classes. Using the Median Test, it was found that a significant difference (0.05 level) existed between these two columns and it can be concluded that individuals of the same age-class spar together more frequently than individuals of different age-classes. Furthermore, it is seen from these data that when individuals of different age-classes did spar together they were of adjacent age-classes and thus quite similar in body-size. This correlation can be best explained by the observation that, with few exceptions, the younger and smaller bulls retreated when approached by an older and larger bull. The question naturally arises as to how a bull knows its own age and size. Although not clearly understood at this time, it is suggested that a bull knows its own age and size through association with members of his own age-class. This association is begun at a very early age when calves gather together in play groups. It is at this age that size discrimination by the calf would be easiest. Teleologically, a calf would readily perceive that it was the same size as other calves and smaller than all other age-classes. If elk are able to recognize other elk as individuals, as seems quite likely, then the process of association from calf-hood onward is an obvious one. The individual has an image of itself in all other elk of its own age-class which it recognizes as individuals. With this image it is possible that fine discrimination in body size and antler development could be made and thus distinctions in age-class made.

A Spearman Rank Correlation Coefficient was computed for the data in Tab. 4 under the column for individuals of the same age-class. This coefficient was significant at the 0.05 level. We can thus conclude that older bulls spar more frequently than do younger bulls, *i. e.*, there is a direct correlation between age and sparring frequency. This might be attributable to the higher levels of testosterone which, presumably, exist in the older males and which in many mammals directly affect aggression.

(II) Diurnal and "seasonal" variation

The data on diurnal variation in the frequency with which sparring occurred are summarized in Fig. 7. It is seen from this figure that there are two obvious peaks of sparring activity, one in the morning (0531—0730 hours) and one in the late afternoon beginning at about 1531 hours and reaching a peak between 1731 and 1930 hours.

The study period was subdivided into three two-week periods and one three-week period in an attempt to demonstrate the "seasonal" changes in the frequency with which certain behavior patterns were seen. These data are summarized in Fig. 8. A more complete discussion of this variation is given below. However, it is emphasized here that there was a marked "seasonal" difference in the frequency of sparring, with a peak occurring between 22 September and 5 October.



ig. 7: Diurnal variation in frequency of sparring activity

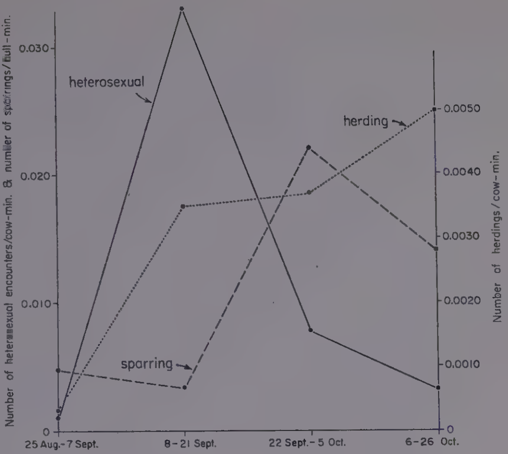


Fig. 8: Seasonal variation in frequency of heterosexual, sparring, and herding encounters

(III) Spatial defense

At no time during this study was there any indication that territoriality existed among elk. This is using the term territoriality as defined by Pitelka (1959) in which an individual or social group of a species utilizes an area to the exclusion of conspecifics, regardless of the spacing mechanism employed in maintaining this exclusiveness. A harem bull certainly does defend the area which his harem occupies, but this area is not fixed geographically. Perhaps this should be referred to as a defended harem space. On several occasions different bulls and harems were seen occupying the same areas at different times and in full view of the elk who had previously occupied the area. Although Graf (1956) contends that the elk of the Oregon coast are territorial, he does not present the critical data on the exclusive utilization of an area by an individual or herd of elk necessary to demonstrate the existence of territoriality.

e) Extending Head

This pattern was most commonly displayed by harem bulls toward cows and calves as the bulls herded them. In this pattern a bull extended his head such that it was level with or slightly below his shoulders (Fig. 9). He

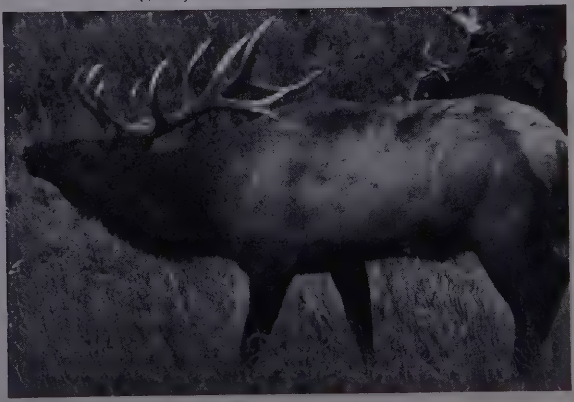


Fig. 9: A bull older than 3½ years displaying a high intensity form of "extending the head"

held his muzzle horizontally. In mild or low intensity forms of this pattern, the bull's head was slightly above the level of his shoulders. However, in such forms his head was still extended and his muzzle held horizontally. In a typical form of extending the head, the ears were extended laterally and perpendicular to the bull's longitudinal axis with the orifices directed anteriorly. However, on some occasions, the ears were tilted back slightly with their orifices directed laterally. Throughout herding a bull's mouth was closed. Palpitation of the penial region sometimes accompanied herding. While maintaining this posture, a bull would rush toward the cows and calves employing a trot or gallop. On one occasion a bull was seen to bob his head and antlers toward the cows and calves. In this variation the bull's muzzle nearly touched the ground. Such bobbing was very similar, if not identical, to the bobbing associated with sparring. On one occasion subsequent to herding, a bull ejaculated.

Extending the head, as a means of herding cows and calves, was displayed only by bulls that were older than 3½ years and in possession of a harem. In addition, however, cows infrequently directed this gesture toward other cows. When displayed by cows this gesture was seen in its simplest form. The head was level with or slightly below the shoulders and the muzzle was horizontal.

The cows and calves responded to this pattern when it was employed in herding by moving away rapidly from the proximity of the bull. They sometimes ran away from the bull and the harem, but usually they rejoined the core of the harem, whereupon the bull ceased herding. The response of a cow to this pattern when displayed by another cow was to move away rapidly from the displayer.

Extending the head was, apparently, a threat gesture. When employed by a harem bull toward cows and calves, it facilitated the cohesion and thus the possession of his harem by herding them together. On the other hand, when directed by one cow toward another cow in a supplantation encounter it presumably alleviated a more intense encounter that might have resulted in physical injury to one or both cows.

(I) Diurnal and "seasonal" variation

The following data concern frequencies of the extending head pattern only as it was employed by harem bulls to herd cows and calves. It is therefore herein refered to as herding. Fig. 10 demonstrates that at least two peaks of herding activity occurred throughout the day. The first of these peaks occurred in the morning between 0731 and 0930 hours and the second occurred in the afternoon between 1531 and 1730 hours. The impression was gained that the frequency of herding was directly influenced by the number of cows present in the harem. The more cows present, the greater was the frequency of herding. In attempt to correct for this variable, the data are expressed as the number of herdings per cow-minute. Cow-minute represents the product of the number of cows in a group and the number of minutes this group was observed.

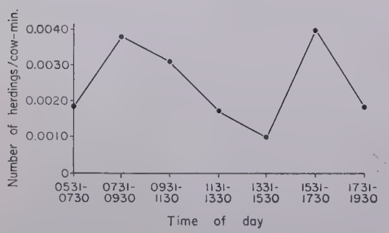


Fig. 10: Diurnal variation in frequency of herding activity

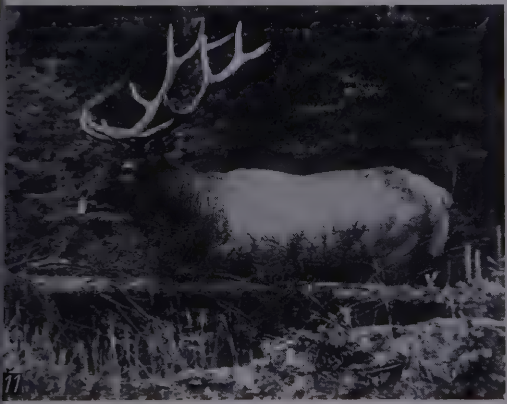
"Seasonal" changes in the frequency of herding are summarized in Fig. 8. ere is at least an extended plateau of herding activity beginning in early ptember (8—21 September) and lasting until late October (6—26 October) en this study was terminated. In addition, the data somewhat suggest a cond and higher peak in the period from 6—26 October. A more complete scussion of this variation is given below.

f) Heterosexual Behavior

Included within this subcategory are several discrete behavior patterns at occurred in social interactions involving at least one member of each sex.

(I) Sexual approach

When a bull approached a cow in a sexual manner his head was held upght with his muzzle tilted downward at about a 45° angle. His ears were eld upright with their orifices directed laterally or anteriorly. Almost inariably a bull flicked his tongue as he approached a cow, moving it in and ut of the mouth in rapid succession. The mouth was closed and the lips were ot retracted (Fig. 11). With only one exception tongue flicking was associated with a sexual approach*). Palpitation of the penial region was commonly associated with a sexual approach. On some occasions a bull was heard to give a popping sound as he approached a cow in the above manner. This may be the same sound that was described by Murie (1951) as "... a peculiar 'tapping' or clucking, with a liquid quality, ..." In a typical bout several pops were given in rapid succession. The bull's mouth was held open throughout a poppng sequence both during and between pops. His lips were not retracted. A exual approach was followed by at least one of the following patterns.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ig. 11: The sexual approach as demonstrated by a harem ull. Note the normal position of his head and the tongue icking

(II) Muzzling

Subsequent to a sexual approach a bull commonly muzzled the perineum f the cow or calf that he had approached (Fig. 12). While thus muzzling a ow or calf a bull sometimes flicked his tongue onto the perineum. This flicking vas virtually the same as tongue flicking described above. Bulls $1^1/_2$ years r older were seen to muzzle the perineums of cows. On some occasions the ow looked along her side toward the bull as he muzzled her perineum.

Muzzle-muzzle contact was commonly associated with heterosexual beavior. As implied, the muzzles of bull and cow were in contact. Following a sexual approach a bull sometimes continued to flick his tongue as he made muzzle-muzzle contact with a cow and thus licking her muzzle. In addition, young cows and calves were seen to make muzzle-muzzle contact with older cows (Fig. 13). The latter type of muzzle-muzzle contact was surely not of a sexual nature.

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*) On one occasion a solitary bull was seen to flick his tongue while standing in a vallow.

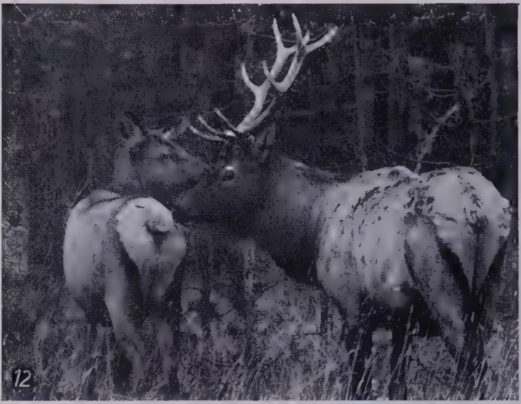


Fig. 12: A young bull muzzling the perineum of a cow

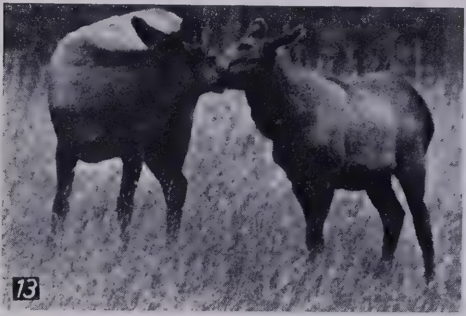


Fig. 13: A cow and calf making muzzle-muzzle contact

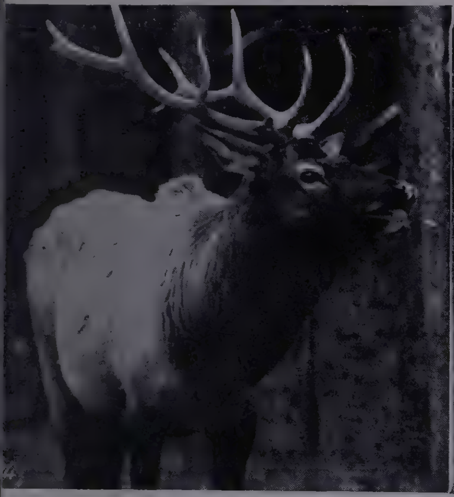
In addition, a bull sometimes flicked his tongue onto the face, neck, and/or body of a cow. In all of these types of muzzling the cow was either standing or recumbent. Her response to muzzling was variable. She remained standing, recumbent, walked away, or demonstrated some of the patterns described below.

(III) Holding mouth open

This pattern was most commonly seen in bulls that were $2^1/_2$ years or older. Spikes were seen giving this pattern on two occasions only. The pattern was preceded by the bull muzzling the ground, frequently where a cow had recently been lying, or muzzling the perineum of a cow. In holding mouth open a bull raised his muzzle slightly above the horizontal plane. His mouth was held open, but his lips were not retracted or curled. Sometimes the preorbital gland was opened widely, especially in older bulls (Fig. 14 and 15). He held this posture for several seconds without moving or emitting any sound. This posture appeared very similar to that assumed while whistling and, except for the open mouth and immobility, very much like the herding posture.

Sometimes this pattern was followed by the bull digging with his antlers and pawing the ground. In such cases the bull also ejaculated.

Apparently, this pattern (holding mouth open) is the same as that described by Schneider (1930) as Flehmen (lip curling) even though the lips were not curled or retracted in elk as in a great many bovids. Schneider distinguished two motivationally different types of Flehmen in captive elk. One was related to sexual odors (Naserümpfen) and the other was, apparently, a form of aggression toward the human observer (Wutgebärde). It was my mpression that the holding mouth open pattern was evoked only by the lfactory stimulus of an estrous female.



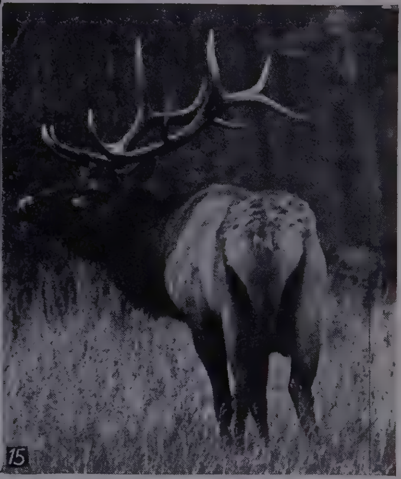


Fig. 14: A young bull displaying the Holding Mouth Open posture, the preorbital gland s only slightly open

Fig. 15: A harem bull, older than 3½ years, in the Holding Mouth Open posture. Note that his preorbital gland is opened widely in contrast to the young bull of Fig. 14

(IV) Muzzling of inguinal region

On one occasion a cow was observed to muzzle the inguinal region of a bull. She did this by placing her muzzle around the anterior surface of the bull's right hindleg and into his inguinal region. The duration of this pattern was very brief (about two seconds). The bull walked away from the cow. This pattern was displayed after the bull had approached the cow.

(V) Jawing

In this pattern the displayer opened and closed her mouth in rapid succession. She sometimes did this with her head and muzzle lowered near the ground. On other occasions the head was moved back and forth laterally while jawing. Subsequent to jawing the displayer sometimes flicked her tongue a few times.

Jawing was demonstrated only by cows. It was most frequently seen as a cow moved away from a bull who was approaching her and flicking his tongue. Jawing was also seen as a bull muzzled a cow's perineum. In such cases the cow looked along her side toward the bull who stood behind her and jawed toward him. Infrequently jawing was observed in a non-sexual context, when a cow jawed as she held her head low and trotted away from another cow who was threatening her (see agonistic section below).

These observations lead me to conclude that jawing was an appeasement or submissive gesture which inhibited any further interaction with the individual to whom it was displayed.

(VI) Lowering head

In this pattern the displayer lowered her head until her muzzle was very near the ground. Her ears were tilted backward slightly against the back of her head and neck. While maintaining this posture the displayer trotted or walked away rapidly from the individual who evoked this pattern (Fig. 16).

This gesture was demonstrated only by cows. It was most commonly seen in association with jawing as a cow moved away from a bull who approached her while flicking his tongue. Once a cow lowered her head as she moved away from another cow who had threatened her.

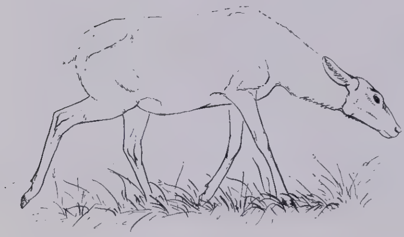


Fig. 16: A cow in the lowering head posture

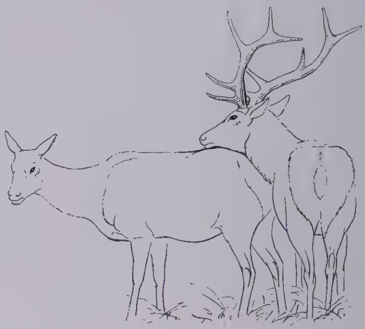


Fig. 17: A harem bull placing his throat over the back of a cow

As with jawing, lowering of the head seemed to be an appeasement gesture that inhibited further interaction with the individual who had evoked the pattern.

(VII) Placing throat over back

Subsequent to a sexual approach and muzzling, a bull sometimes placed the ventral surface of his muzzle and throat over the rump and back of a cow. The bull stood behind or, less frequently, perpendicular to the cow in this pattern (Fig. 17). The cow was either standing or recumbent. Contact between the two was sometimes made. The cow responded either by moving away or by remaining in her position. If the cow remained in a standing position the bull either moved away or mounted her.

Bulls $1^1/_2$ years or older demonstrated this pattern. Cows were the most common recipient of this pattern, calves less frequently, and spikes least frequently.

(VIII) Heterosexual mounting

Heterosexual mounting was observed on five occasions only. On the 15th of September one particular bull and cow engaged in heterosexual mounting at 1040, 1210, and 1622 hours. On the 17th of September a different pair engaged in heterosexual mounting at 1803 hours. The last heterosexual mounting was seen on the 18th of September at 1733 hours. This final sequence might have involved the same bull as on the 15th of September. In a typical bout of heterosexual mounting a bull approached a cow several nes, mounted her incompletely several times, and finally terminated the quence by mounting her completely. The details of this sequence are con- lered in the following paragraphs.

An incomplete mount was always preceded by several sexual approaches, described above. The number of approaches preceding an incomplete mount ried from two to eight. Subsequent to each of these approaches the cow alked away from the bull. In some of the approaches, especially those mmediately preceding an incomplete mount, the bull placed his throat over e rump of the cow. Prior to the incomplete mountings a cow sometimes ked her sides and back. In an additional pattern that sometimes preceded e incomplete mountings, the cow looked over her shoulder toward the bull ho stood behind her. On one occasion while looking at the bull in this anner a cow flicked her tongue.

In a typical incomplete mount a bull approached a cow from behind, icked his tongue onto her perineum, placed his throat over her rump, and se up onto his hindlegs and straddled the cow with his forelegs which were aced just anterior to her hindlegs. With his back arched he slowly moved s hindquarters and erect penis toward the cow's perineum. On some occa- ons the bull's erect penis made contact with the cow's perineum. However, o pelvic thrusts or intromission occurred during an incomplete mount. In ldition, the bull's erect penis sometimes palpitated or jerked along his gittal plane during an incomplete mount. The dismount was accomplished ther by the bull sliding off of the cow or by the cow stepping forward or cking away from the bull.

Throughout a heterosexual mounting bout, especially between incomplete ounts, the bull followed very close behind the cow as she slowly walked way from him. Between incomplete mounts a variety of behavior was emonstrated. The bull sometimes licked and muzzled the cow's neck. Muzzle-uzzle contact and jawing also occurred. The cow who engaged in three bouts f heterosexual mounting on the 15th of September rubbed the bull between complete mountings and prior to the complete mounts. In this pattern she nployed her muzzle, neck, and forehead to rub the bull's neck, sides, hips, nd back. In one extreme form of this rubbing the cow placed one of her orelegs over the bull's shoulders. The other two cows who engaged in hetero- exual mounting were not seen to rub the bulls.

This same cow who rubbed the bull between incomplete mounts demon- trated still another form of behavior not observed in the other two cows. Bet- ween incomplete mounts she employed the stiff-foreleg kick threat (see below) o threaten and supplant another cow. This occurred in all three of her bouts f heterosexual mounting a total of ten times. Similarly between incomplete ounts, this same cow displaced another cow by using the extended head hreat. This type of interaction occurred twice in one bout of heterosexual ounting. In all of these agonistic encounters the estrous cow was being ollowed closely by the bull.

In any one bout of heterosexual mounting there was only one complete ount. Complete mounts were always preceded by incomplete mounts, anging in number from three to seven. The complete mount was virtually he same as an incomplete mount with the following exception. In the com- lete mount when the bull's erect penis touched the cow's perineum or vagina e gave one powerful pelvic thrust. While delivering the pelvic thrust the ull's hindlegs lost contact with the ground and swung forward and outside of the cow's hindlegs (Fig. 18). The pelvic thrust sent the cow lurching forward resulting in the dismount. In some of the complete mounts the cow bucked and apparently kicked the bull in his ventral region with her hindfeet. This bucking was almost simultaneous with the pelvic thrust and, undoubtedly, facilitated the dismount. Thus for a very brief moment the cow supported the entire weight of the bull. At no time throughout a sequence did a cow lower her hindquarters. It was never determined if the bull ejaculated into the cow during these complete mounts. Furthermore, due to the distances at which these observations were made, it was not determined if vocalizations accompanied such heterosexual mountings. In any one bout of heterosexual mounting there was only one pelvic thrust and this occurred only during the complete mount.

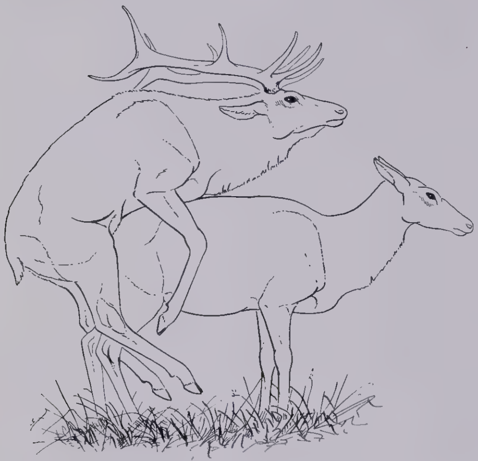


Fig. 18: A harem bull delivering a pelvic thrust to a cow. Note that his hindlegs are off the ground

The duration of bouts of heterosexual mounting from the first sexual approach to the termination of the complete mount ranged from two to twelve minutes with a mean of eight minutes. All the bulls engaging in heterosexual mounts were harem bulls, had six points, and were estimated to be older than $3^{1}/_{2}$ years.

Subsequent to the complete mount the bull and cow stood fairly near to one another for several seconds. Sometimes the cow appeared to stand in a hunched manner with her hindlegs and forelegs unusually close together and her back in an arched or hunched position. On one occasion a clear-colored fluid passed from the cow's perineum immediately after the dismount.

Initially this fluid passed in a steady stream, but ultimately it was passed in spurts. On another occasion after a complete mount the bull moved away from the cow with his head extended, muzzle horizontal and penial region palpitating. He then moved his antlers slowly through a shrub while his penial region continued to palpitate and his penis was erect.

The information in the literature on heterosexual behavior in elk is scant. Altmann (1952) states: "Mounting was seen but not complete copulation." Graf's (1955) description is better, but it is still void of much detail. In describing an encounter between a mature cow and bull he states: "For a second he just stood there and then quickly mounted the cow and copulated. Two subsequent copulations took place, the second one four or five minutes after the first and the last one about thirty seconds after the second one. This last one was of such violence that the cow was driven to her knees with such force as to throw her head first into the tangle of limbs and vines of the windfall in front of her." Graf may have observed two incomplete mounts followed by one complete mount. Graf also mentions that he observed a spike mount and copulate "successfully" with a cow three times.

(IX) Quantitative data on participants

Tab. 5 summarizes the data on the frequencies with which certain pat-rns of heterosexual behavior were observed and the frequencies with which e various age-sex classes were seen to engage in these patterns. More than

Tab. 5: Heterosexual Behavior

Demonstrator of pattern	Name of pattern, recipient, and frequency: Sexual approach		Muzzle-muzzle		Muzzle-perineum		Other forms of muzzling		Placing throat over back		Incom-plete mounts	Complete mounts	Subtotal no. en-counters and per-cent of grand total no. encounters
	cow	calf	cow	calf	cow	calf	cow	calf	cow	calf	cow	cow	
bull >3½ yrs.	348	9	20		70	3	4		39	2	29	'5	357 93.95 %
bull 2½ yrs.	6				3				1				6 1.58 %
Spike	14	3	6		6	3	1		1				17 4.47 %
Column totals	368	12	26		79	6	5		41	2	29	5	380 *

* Grand total no. encounters

ne of these patterns sometime occurred in one encounter. As a consequence. e total number of entries in each row of Tab. 5 do not equal the number of ncounters for the particular row considered. The sexual approach occurred in ll heterosexual encounters and therefore the number of sexual approaches or each row also equal the number of heterosexual encounters for that row. n view of the fact that all harem bulls were older than 3½ years, it is readily nderstandable why the majority (93.95 %) of heterosexual encounters involved bulls of this age-class. The fact that spikes engaged in heterosexual enounters almost three times more than did 2½ year old bulls is probably est explained by the fact that some spikes remained in cow groups (harems) hroughout the rut, whereas for a period of about six weeks, including the eak of the rut, no 2½ year old bulls were seen in cow groups (see section n social structure). Those 2½ year old bulls which did participate in heteroexual encounters were temporarily peripheral to a harem. These encounters ccurred when the harem bull was engaged in some other activity.

(X) Diurnal and "seasonal" variation

The data demonstrating the diurnal encounters are summarized in Fig. 19. The fluctuation in the frequency of heterosexual probability that an estrous cow will be present in a harem is directly related to the number of cows in the harem. In an attempt to correct for this variable, the data are expressed as the number of heterosexual encounters per cow-minute. It is apparent from Fig. 19 that at least two peaks of heterosexual activity occurred throughout the day. The first and lower of the two peaks occurred in the morning between 0931 and 1130 hours. The second and highest peak occurred late in the afternoon between 1731 and 1930 hours. In comparing the time of day at which heterosexual mounting occurred (1040, 1210, 1622, 1803, and 1733 hours) with

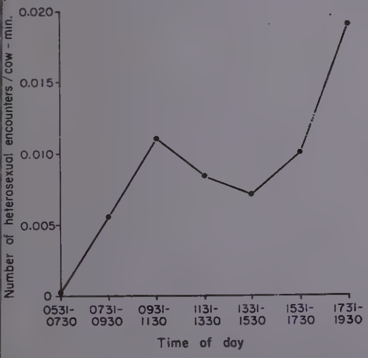


Fig. 19: Diurnal variation in frequency of heterosexual activity

Fig. 19, it is seen that three of these encounters occurred at peaks and that a fourth (1622) also occurred at a relatively high point on the curve.

It can be seen in Fig. 8 that a very sharp and distinct peak of heterosexual activity occurred between 8 and 21 September. This "seasonal" peak is further substantiated by the fact that all five cases of heterosexual mounting occurred between 15 and 18 September.

g) Comparison of "Seasonal" Variation in Sparring, Herding, and Heterosexual Encounters

The peak of heterosexual activity occurred between 8 and 21 September (Fig. 8). The extension or continuation of a high level of herding activity beyond the peak of heterosexual activity is not explicable at this time.

The occurrence of a peak of sparring activity after the peak of heterosexual activity might be best explained in the following manner. Heterosexual behavior was engaged in primarily by bulls older than $3^1/_2$ years. The majority of data on sparring were based on encounters between $2^1/_2$ year old bulls. MURIE (1951) presents information which indicates that $2^1/_2$ year old bulls loose their velvet later in the year than do older bulls. Increased levels of testosterone, apparently, cause the shedding of velvet (TURNER 1955). It seems quite possible, then, that $2^1/_2$ year old bulls do not develop their highest levels of testosterone until one to two weeks after the older bulls. Presumably, as in many other mammals, testosterone has a direct effect on aggression and thus on the sparring frequency of elk, hence the later peak of sparring activity.

h) Homosexual Behavior

Sexual behavior between members of the same sex was rare. On two occasions a spike was seen placing his throat over the rump of another spike. In one of these cases it was reciprocated. In this latter case one spike had velvet on his antlers and the other did not. In the other case both spikes were without velvet. Infrequently, a cow was seen to muzzle the perineum of another cow. Once, two spikes rubbed the sides of their heads together as they stood facing one another. Subsequent to this one of the spikes rubbed his muzzle over and then under the muzzle of the other spike.

Other Social Behavior

Included in this section are descriptions of behavior patterns that probably were not restricted to nor characteristic of the rut.

a) Agonistic Behavior

Included within this subcategory are several discrete behavior patterns that occurred in social interactions in which one or both participants could have or did receive physical injury.

(1) Displacing (supplanting)

In the simplest and most common form of displacing, one individual (displacer) walked toward another (displacee). The displacee walked away from the place in which it had been feeding, standing, or lying as the displacer came near. The displacer then stood, fed, or lay where the displacee had been. In all cases of displacement the displacee looked away from the displacer.

On some occasions the displacee jumped to one side and then moved away rapidly when the displacer came near. On a few occasions recumbent cows and calves were approached by a bull who gently touched them on their ack with one of his forefeet. The recumbent individual moved away and he bull lay in the newly vacated space. A variation of this form of displacement was seen on one occasion when a bull kicked a recumbent cow on her eck with one of his forefeet. She promptly moved away and he lay where he had been. In all of these cases the bull muzzled the ground prior to ying down.

Only 11 cases of displacement were observed in detail, thus prohibiting ny generalizations about the frequency with which the various age-sex classes displaced one another. However, the limited observations demonstrate that bulls older than $3^{1}/_{2}$ years displace cows and calves, $2^{1}/_{2}$ year old bulls displace one another and spikes, and cows displace one another and calves.

It is not certain what the significance of such displacements was. Howver, it seems quite reasonable that displacement encounters among elk, as with many other mammals, serve to reassert dominance relationships which n turn alleviate or at least reduce the frequency with which social interactions esulting in physical injury to one or both participants occur.

Altmann (1956) mentions that elk displaced one another from sheltered areas during storms. Such displacement "... was accomplished by mere gesture. In cows, the gesture of threat consisted of empty beats with the front feet. In bulls a shaking of the antlers with lowered head was the gesture of hreat." It is not clear to me what she means by "empty beats" nor is her description of the bull's gesture of threat reminiscent of any pattern I observed.

(II) Kicking toward with stiff foreleg

In this pattern one foreleg was extended forward and then brought down and back rapidly. The leg was held stiffly throughout the kick. The ears of the displayer were flattened against the back of its head and neck. The head was held upright and the muzzle nearly horizontal. Rarely, the displayer of this pattern actually kicked the displayee (making physical contact). In a typical encounter no physical contact was made. The displayee usually responded to this pattern by moving away rapidly from the displayer. This pattern was directed by cows toward cows, cows toward calves, and calves toward calves. Kicking toward with a stiff foreleg apparently functioned as a threat gesture.

(III) Elevating muzzle

The displayer of this pattern held its muzzle upward at about a forty-five degree angle. Its ears were flattened against the back of its head and neck with their orifices facing outward (laterally) (Fig. 20b & c). The displayer and displayee were close together being about three to four feet apart. The displayee responded by moving away. Sometimes both participants elevated their muzzles toward one another simultaneously. In such cases one or both participants eventually moved away. Although elevating the muzzle was sometimes followed by kicking with a stiff foreleg or by the extended-head threat, it was more typically followed by the displayer rising up on its hindlegs and kicking with its forelegs toward the displayee (see below, and Murie 1951, Graf 1955, and Altmann 1956).

Elevating the muzzle was demonstrated by cows toward cows, cows toward calves, calves toward calves, and spikes toward spikes.

It seems quite feasible that elevating the muzzle represented an incipient rise to the hindlegs (see below) and thus functioned as a threat gesture.

(IV) Rising on to hindlegs

In this pattern the displayer elevated its muzzle to about a forty-five degree angle as described above and then while maintaining this posture rose up onto its hindlegs. The degree to which the forequarters were elevated varied, but never did the displayer stand vertically erect on its hindlegs. While standing upright on its hindlegs the displayer sometimes pawed or kicked with its forelegs toward the displayee (Fig. 20d & e). On one occasion only was the displayer seen to actually kick the displayee. On most occasions the displayee moved away rapidly (see MURIE 1951 and GRAF 1955).

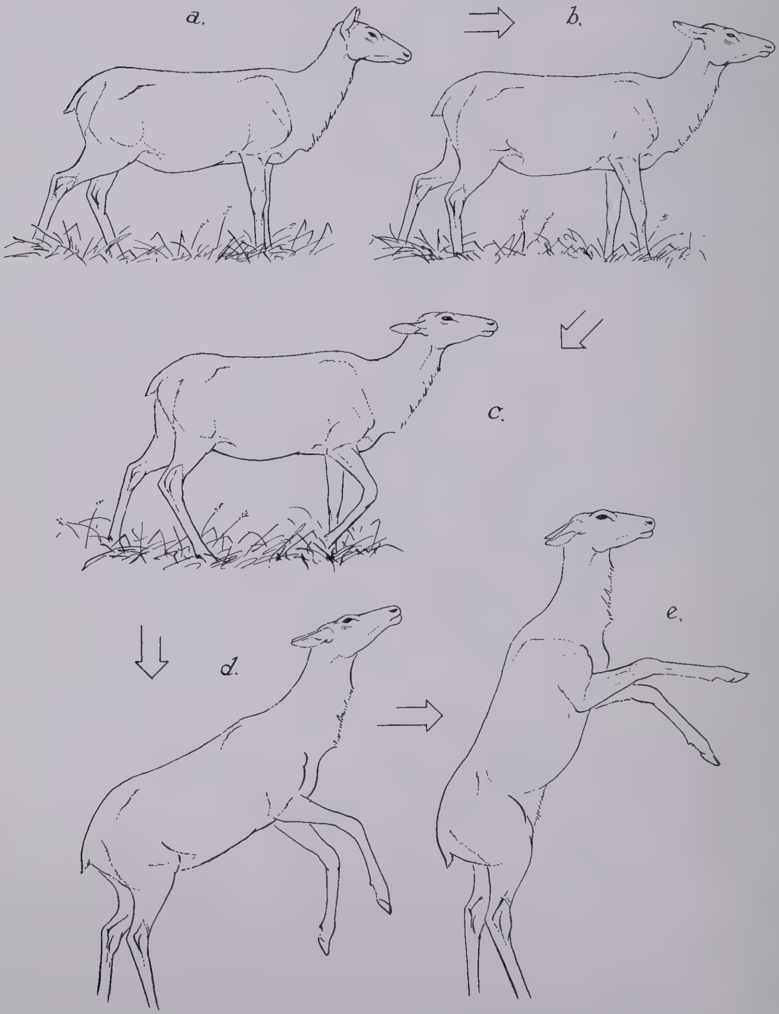


Fig. 20: Stages in a graded threat-gesture system as displayed by a cow. a) Normal posture. b) Low intensity threat, note slight elevation of muzzle and lowering of ears. c) More intense threat, muzzle is elevated higher and the ears lower than in preceding posture. d) Higher intensity threat, a slight rising on to hindlegs. e) Highest intensity threat, rising on to hindlegs and kicking with forelegs

This pattern was demonstrated by cows toward cows, spikes toward ikes, and calves toward calves.

Rising up on the hindlegs, undoubtedly, functioned as a threat gesture. pparently, many intermediate patterns exist between elevating the muzzle d kicking while standing upright on the hindlegs. It is suggested that these o extremes and all of their intermediate grades represent a continuous or aded system of signalling (see Hockett 1960).

(V) Quantitative data on frequency and participants of non-contact agonistic encounters

The data on agonistic encounters not involving physical contact are mmarized in Tab. 6. Presented in this table are the actual number of en- unters observed and the number of encounters per pair-minute. The ratio- le and explanation of the pair-minute have been discussed in the section sparring. Data on the following patterns are included in Tab. 6: chasing, ead bobbing, kicking toward with stiff foreleg, elevating muzzle, extending ead*), and rising on hindlegs. It is of interest to note that all agonistic ncounters observed involved only two individuals. Multipartite encounters ere never seen.

Tab. 6: Non-contact Agonistic Encounters

No. encounters
No. encounters / pair-min.

	Aggressee						
	Bull >3 1/2 yrs.	Bull 3 1/2 yrs.	Bull 2 1/2 yrs.	Spike	Cow	Calf	Total
Bull >3 1/2 yrs.	3 0.027		10 0.0031	25 0.0068			38
Bull 3 1/2 yrs.			1 0.00017				1
Bull 2 1/2 yrs.			2 0.00024	8 0.0016			10
Spike							
Cow				1 0.000025	34 0.00011	2 0.000012	37
Calf						1 0.000043	1
Total	3	0	13	34	34	3	87

In considering the data of Tab. 6, greatest emphasis will be placed on e ratios of the number of encounters per pair-minute. All of the encounters which a bull older than 3½ years was the aggressor consisted of a harem ull chasing other bulls. Presumably, bulls older than 3½ years represented greater threat to a harem bull than any other age-class, thus accounting for e greater frequency of encounters between bulls of this age-class (see also ction on sparring). As emphasized in the section on social structure, spikes emained in cow groups (harems) throughout the rut. Although spikes were tolerated” more than any other bull class by the harem bulls, the fact that ey came into contact with harem bulls more frequently than the other bull classes accounts to a large extent, if not completely, for the observation that harem bulls chased spikes so often. On the other hand, the $2^1/_2$ year old bulls remained away from the cow groups, or at best on their periphery, for nearly six weeks. Furthermore, it seems quite certain that $2^1/_2$ year old bulls represented little threat to a harem bull.

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*) The data on extending head when it was employed by a harem bull to herd cows d calves is not included here (see section on extending head).

87.5 % of the encounters in which a $2^1/_2$ year old bull aggressed against a spike involved head bobbing. The aggression of $2^1/_2$ year old bulls against spikes may have been due to the close association of these two age-classes in bull groups.

The fact that cows and calves were not watched as closely as the bulls undoubtedly accounts to a great extent for the relative infrequency of agonistic encounters among these classes. However, in spite of this inadequacy in sampling it seems of significance that calves were involved in agonistic encounters only with cows and other calves. Furthermore, excluding the herding encounters and one exceptional case, cows only engaged in agonistic encounters with calves and other cows.

With possible exceptions existing among the age-sex classes of cows and bulls older than $3^1/_2$ years, the aggressor was always the same age or older than the aggressee.

(VI) Comparison of analyses of sparring and non-contact agonistic encounters among males $1^1/_2$ years or older

The categories of sparring and non-contact agonistic encounter are mutually exclusive. If threat gestures, *e. g.*, head bobbing, chasing, were followed by sparring the encounter was classed as one of sparring. If such gestures were not followed by sparring the encounter was classed as a non-contact agonism. It was demonstrated in the section on sparring that bulls of the same age-class sparred together more frequently than did bulls of different age-classes. A Median Test conducted on the data for spikes and the other three bull age-classes demonstrated that there was no significant difference (0.05 level) in the frequency with which bulls of the same age-class and bulls of different age-classes participated together in non-contact agonistic encounters. Apparently, if bulls of the same age-class threatened one another a sparring encounter usually ensued. However, if an older bull threatened a younger bull the younger retreated, no sparring ensued, and the encounter was classed a non-contact agonism. At least one notable exception to this generalization existed. Bulls older than $3^1/_2$ years not only sparred together more frequently, but also engaged in non-contact agonistic encounters more frequently than any other age-class. This exception, undoubtedly, accounts for the lack of a significant difference in the frequency of non-contact agonistic encounters between bulls of the same age-class and bulls of different age-classes.

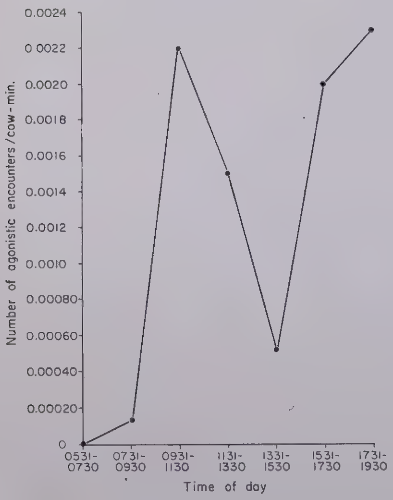

Fig. 21: Diurnal variation in frequency of agonistic activity

(VII) Diurnal variation

Approximately 90 % of the non-contact agonistic encounters were oberved in cow groups (harems). In demonstrating the diurnal variation in the requency of non-contact agonisms, only the data from the cow groups were onsidered. The variables of observation time and group size are corrected or by the factor of cow-minutes. It is apparent from Fig. 21 that at least two eaks of non-contact agonistic activity occurred. The first of these peaks ccurred in the morning between 0931 and 1130 hours and the second between 731 and 1930 hours in the afternoon.

(VIII) Comparison of diurnal variation in several patterns of behavior

In comparing the data on diurnal variation in frequency of whistling, parring, herding, heterosexual encounters, and agonistic encounters (see preeding sections) it is observed that, with the possible exception of whistling, ll of these patterns of behavior had at least two diurnal activity peaks. These eaks occurred in the morning between 0531 and 1130 hours and in the afteroon between 1531 and 1930 hours. All of these patterns were low in their requency of occurrence at midday. Excluding whistling*), this low occurred or all patterns between 1331 and 1530 hours. It seems obvious then that there xists an underlying diurnal periodicity affecting the frequency of several ehavior patterns.

b) Grooming

Grooming was a social activity in which one elk licked another. The ears, ace, and neck were the areas groomed. Simultaneous mutual grooming was ot observed. Cows groomed calves and other cows, and calves groomed cows. n addition to grooming, individuals were seen to clean themselves. In so oing they nibbled as well as licked their pelage. Nearly every area of the ody except the ears, face, and neck were self-cleaned in this manner. Infreuently, elk rubbed their necks and faces on saplings, presumably as a variaion of self-cleaning (see GRAF 1955, ALTMANN 1956).

c) Suckling

In this pattern the suckler flexed its legs, especially its forelegs, and iniially butted the udder with its muzzle. If the suckler was relatively large it nelt on its forelegs. Sometimes the suckler butted the udder intermittently hroughout the suckling sequence. The cow stood and/or fed throughout the ncounter and usually terminated the sequence by walking away. The most ommon form of suckling encounter involved an adult cow and a calf that ras four to six month old. However, on some occasions what appeared to e 1½ year old cows suckled from older cows.

d) Play

Play was most commonly seen among calves and in the majority of cases ras a social activity in that two or as many as six calves played together. lthough play situations were obvious to the author, the phenomenon of play s not easily defined. The impression was gained that play situations differed rom non-play situations in temporal pattern and in the apparent fact that rrelevant or unrelated behavior patterns occurred together during play (see IEYER-HOLZAPFEL 1956).

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*) Whistling is excluded because its frequency of occurrence was recorded only etween 0700—0900, 1100—1300, and 1700—1900 hours.

Many of the behavior patterns seen in play situations were also demonstrated by older elk in non-play situations. Stotting (see section on alarm), alert trotting, elevating the muzzle, and kicking toward with a stiff foreleg were such patterns. In addition, there were two patterns that seemed unique to play. Gamboling was a gait in which the hindlegs were kicked backward in unison and as they were brought forward the forelegs were kicked forward. This sequence was repeated several times in rapid succession giving a bucking appearance. Gamboling also occurred at the termination of some sparring encounters (see above). In sparring situations it was difficult to categorize the encounter as play or non-play. The other pattern unique to play was circling in which the individual rapidly turned in circles with its head and muzzle turned and directed posteriorly along one side toward its hindquarters. Circling was observed on one occasion only (see wallowing above). In a typical play encounter the participants demonstrated some or all of the above patterns as they chased and counter-chased one another.

Although play was primarily an activity of calves, it was seen infrequently and less distinctly among elk that were $1^1/_2$ years old (see MURIE 1951). In the majority, if not all, of the cases only elk of the same age-class played together.

e) Alarm

When faced with potential danger (usually the author) the elk showed one of three responses. The most common response was immediate flight. While fleeing the elk employed either the gallop or alert trot. The alert trot is well illustrated by MURIE (1951). In this gait the individual held its head and ears erect and its muzzle nearly horizontal. Alert trotting was demonstrated by all age-sex classes. The alert trot seemed to evoke flight in other elk and, undoubtedly, communicated the proximity of potential danger.

The second most common response was the alarm bark (see MURIE 1932). This call was of short duration, high amplitude, and was begun and terminated abruptly. Typically, barks occurred as a series of two or more with variable time intervals between individual barks. Sonagrams of alarm barks are presented in Fig. 22. It is apparent from these sonagrams that the alarm

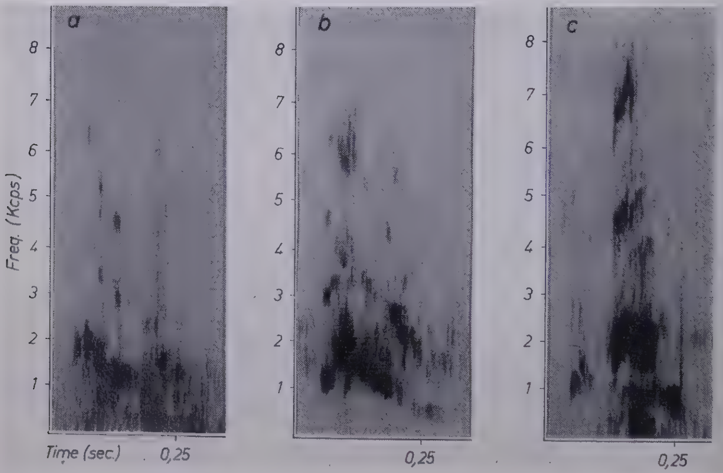

Fig. 22a, b: Alarm barks of cow elks; c: Alarm bark of a bull older than 3½ years bark of a cow and a bull were different. Audibly, the alarm bark of a bull was of higher pitch (frequency) than that of a cow. The major energy of a cow's alarm bark occurred between 0.080 and 3 Kcps. Whereas that of a bull occurred not only between 0.080 and 3 Kcps, but also between 4 and 5 Kcps and between 6.5 and 7.5 Kcps. The occurrence of major energy in these higher frequencies accounts for the audible impression of a higher pitched call in the bull. In both cows and bulls the duration of the alarm bark was about 0.25 seconds. The mouth of the vocalizer was opened slightly, but its lips were not retracted during this call. Throughout such an encounter the vocalizer stared toward the source of disturbance. This alarm response sometimes lasted for several minutes. Alarm barks were given by adult cows and bulls. It was not determined if elk younger than 3¹/2 years were capable of giving this call or not. On at least one occasion as a bull gave alarm barks he ejaculated. It seemed that alarm barks first directed the attention of other elk to the vocalizer and then towards the direction in which the vocalizer was staring and the source of disturbance. Several times elk approached, gathered around, and looked in the same direction as the vocalizer.

The third response to potential danger was uncommon. It is a gait that has been termed stotting (MABERLY 1962). In this pattern all four legs were moved backward and forward in unison and in a rather stiff manner giving the appearance of a bouncing gait. The head and ears were held upright and the muzzle was nearly horizontal. This pattern occurred only six times, being demonstrated by 15 individuals. Half of these occasions were alarm situations and half were play situations. In two of the alarm situations a cow that was older than $1^1/_2$ years stotted when alarmed by the author. In the third alarm situation a spike stotted away as a large, solitary, six-point bull chased him. The three play situations involved nine calves, two spikes, and one cow who was $1^1/_2$ years old (see wallowing above for latter three). The function of stotting is not apparent. Conceivably, by elevating the head stotting facilitates the visual vantage or, as with alert trotting, it communicates to other elk the proximity of potential danger. Stotting as it occurs in elk is very similar, if not identical, to the stotting gait of mule deer *(Odocoileus hemionus)* and some of the bovids of East Africa such as oribi *(Ourebia ourebi)*, Thomson's *(Gazelle thomsoni)* (see MABERLY 1962), and Grant's gazelle *(Gazelle granti)*. Stotting has also been described in elk by MURIE (1951) who observed it in late winter also and by YOUNG and ROBINETTE (1939) who ascribed this gait to young animals in a playful mood.

It is tentatively suggested that the differential alarm response of elk is based on the physical nature of the alarm stimulus. Alarming olfactory stimuli evoke immediate flight, alarming auditory stimuli evoke immediate flight or alarm barks depending on the distance between the stimuli and elk, and alarming visual stimuli evoke alarm barks. The distinction between the stimuli evoking stotting and alert trotting is not apparent.

f) Group Cohesion

On several occasions when a group of elk had been temporarily divided and some of its members were visually separated from one another, a squealing-like call was heard. MURIE (1932) describes this call as "E-e-e-e-e-uh!" and GRAF (1955) describes it as "eeyyh" or "eeeyuh." In a typical case the elk who were separated from one another exchanged cohesion squeals several times until they were reunited. It was most commonly heard between cows and calves. However, on one occasion it was verified that a large, six-point harem bull gave this call as he moved toward his harem after being temporarily separated from them. On this occasion I imitated the bull's squeal. The bull and I exchanged squeals several times until the bull came through the dense vegetation to within 30 feet of me, whereupon he moved away and rejoined his harem. It seems reasonable to assume that this squealing facilitated the reunion of elk and thus the cohesion of the group.

g) Group Progressions

Sometimes as a cow group fled from me or as they slowly moved across an open hillside they did so in a linear and orderly manner. In such progressions it seems quite feasible that the animal in the first position of the column was the leader, directing the movements of the group. Twelve such progressions were observed in detail. In all twelve cases a fully mature cow was at the head of the progression. In one of them no bulls or spikes were present in the group. In nine cases bulls that were at least 3¹/₂ years old were present in the group. Spikes were present in seven of the twelve progressions. Although not conclusive, these data strongly suggest that a cow group's movements were determined by an adult cow(s) and not by the bulls or spikes. This conclusion is in agreement with Altmann (1952) who states: "The leading elk cow and other mature females took the preferred places at the lick and regulated the length of stay as well as the direction of travel on leaving the lick."

Individual Sampling

In addition to systematically describing the behavior as it was observed and recording the frequency with which certain patterns occurred, a method of individual sampling was employed. In the individual sampling a particular elk was continuously watched for a specific amount of time. The duration and sequential order of each behavior pattern that the individual demonstrated was recorded. Individual sampling was done of elk from six different classes, namely: cows, spikes in velvet, spikes without velvet, 2¹/₂ year old bulls, solitary bulls older than 3¹/₂ years, and harem bulls older than 3¹/₂ years. Individual sampling was conducted at three different times of the day: 0700—0900, 1100—1300, and 1700—1900 hours. I attempted to obtain 60 minutes of sampling for each of the six classes at each of the three times of day. Thus, a total of 180 minutes of sampling was sought for each of the six classes. Furthermore, I sought to sample three different individuals at each of the three times of day for each of the six classes, *i. e.*, I tried to sample nine different elk for each of the six classes. Ideally, then, each individual would have been sampled for 20 minutes. The actual sampling times closely approximated the sample times sought and, as a consequence, it can be considered that the six classes of elk were uniformly sampled. Furthermore, by expressing the data as percentages the slight differences in sampling time are virtually eliminated. Due to the fact that extensive variation occurred within some of the age-sex classes in terms of the percentage of time spent on certain activities, the data have been pooled for each age-sex class.

The results of individual sampling are summarized in Tabs. 7 and 8. These data represent mean percentages and it should be emphasized that the variation within a class sometimes exceeded the variation between age-sex classes. In Tab. 7 it is obvious that bulls older than 3¹/₂ years spent considerably less time feeding than other classes. Excluding the solitary bulls older than 3¹/₂ years, the harem bulls fed half as much or less than any other class.

Correlated with this is the fact that bulls older than $3^1/_2$ years spent more time walking and engaging in other activities than the other classes. Tab. 8 demonstrates that harem bulls spent about 15 % of their time in herding, heterosexual behavior, thrashing and digging, and whistling. With the possible exception of whistling, all of these activities probably have high energy requirements. A similar pattern, with the exclusion of herding and heterosexual behavior, seemed to prevail for solitary bulls older than $3^1/_2$ years. In addition, harem bulls stood about twice as long as any other age-class. Although standing is a relatively inactive pattern, it, undoubtedly, requires more energy than a pattern such as lying, which harem bulls indulged in half as much as standing and less so than several other classes.

Tab. 7: Distribution of Time Among Various Activities* as Related to Age and Sex

	Cow	Spike in velvet	Spike - no velvet	$2^1/_2$ yr. bull	Solitary >$3^1/_2$ yr. bull	Harem >$3^1/_2$ yr. bull
Running		0.048 %		0.58 %	0.31 %	0.084 %
Walking	0.87 %	1.90 %	3.67 %	2.71 %	7.75 %	9.15 %
Threatening or being threatened	0.28 %	0.38 %	0.14 %	1.42 %	0.048 %	0.50 %
Feeding	45.69 %	37.97 %	62.59 %	47.71 %	27.04 %	17.18 %
Self - cleaning	0.093 %	0.52 %		0.13 %		
Standing	18.39 %	8.60 %	10.89 %	19.77 %	15.80 %	36.91 %
Lying	34.40 %	49.91 %	20.73 %	21.24 %	39.40 %	19.12 %
Other *	0.28 %	0.67 %	1.98 %	6.44 %	9.65 %	17.06 %

* See Tab. 8

Tab. 8: Distribution of Time Among Other* Activities as Related to Age

	Spike in velvet	Spike - no velvet	$2^1/_2$ yr. bull	Solitary >$3^1/_2$ yr. bull	Harem >$3^1/_2$ yr. bull
Herding					3.85 %
Heterosexual encounter	0.33 %	1.47 %			6.68 %
Sparring		0.23 %	0.22 %		
Thrashing and digging with antlers		0.18 %	6.18 %	3.72 %	2.42 %
Whistling			0.044 %	4.97 %	2.36 %
Holding mouth open (flehmen)	0.33 %	0.10 %		0.87 %	0.55 %
Standing with penis palpitating				0.096 %	1.20 %

* See Tab. 7

The preceding interpretations of the data in Tabs. 7 and 8 allow one to hypothesize that bulls older than $3^1/_2$ years (especially harem bulls) are acquiring less energy than they are expending. As a consequence, these bulls develop a negative energy balance during the rut. This is in harmony with Murie's (1951) conclusion that: "During the rut the bulls do not eat so much as formerly, and the actively breeding ones indulge in such tremendous expenditures of energy that when the rut is over, the surplus fat is gone and winter finds them in poor condition. The cows, on the other hand, feed regularly during the rut."

Acknowledgements

This study was financed by a contract from the Canadian Wildlife Service, Department of Northern Affairs and National Resources. I am especially grateful to Dr. W. E. Stevens and Mr. D. R. Flook of the Canadian Wildlife Service, Edmonton, Alberta for their assistance and cooperation in the initiation of this project. The advice and assistance of Mr. Flook throughout the study was greatly appreciated. I am also indebted to Mr. G. H. L. Dempster, General Park Superintendent and Mr. Robert Hand, Chief Warden of Banff National Park, for permission to study in the park. Thanks are also extended to Mr. Ed Carleton and Mr. Hugh Jennings, wardens at Banff, who were most helpful in providing information on the location of elk in the park. Dr. Peter Marler of the Department of Zoology, University of California, Berkeley provided the funds (NSF Grant GB 4479) for the preparation of the manuscript. I am also grateful to Dr. Marler and to Drs. F. Nottebohm and D. McCullough for their comments on the manuscript. The drawings were done by Mr. Gene Christman.

Summary

Qualitative and quantitative information on elk behavior are presented. These data were obtained during a two month study of elk during the 1965 rutting season in Banff National Park of the Canadian Rockies. The major findings and conclusions are as follows.

1. Detailed descriptions of certain behavior patterns are presented.

2. The size of cow groups decreased with the onset of the rut and then increased with the waning of the rut. The percentage of cows and calves in the groups remained relatively stable. The percentage of spikes, 2¹/₂ and 3¹/₂ year old bulls decreased as the rut progressed and increased as the rut waned. Spikes remained in the cow groups longer and rejoined them sooner than did the 2¹/₂ and 3¹/₂ year old bulls. With the onset of the rut bulls older than 3¹/₂ years joined the cow groups, splitting them into smaller groups, and driving out the 2¹/₂ and 3¹/₂ year old bulls.

3. Sonagrams and other quantitative data on whistling (bugling) are presented.

4. It is suggested that whistling, thrashing and digging, and wallowing are methods whereby bulls attract one another. The adaptiveness of such attraction lies in the resulting sparring encounters and their facilitation of sexual selection.

5. Bulls 3¹/₂ years "ejaculated" while: whistling, thrashing, digging, standing in wallows, after herding, and while giving the alarm bark.

6. Intense sparring encounters were rare. The infliction of a body blow occurred only once. Wounds derived from sparring probably play a minor role in elk mortality. Males of the same age-class sparred together more frequently than did males of different age-classes. Older bulls sparred more frequently than did younger bulls. Diurnal and "seasonal" variations in the frequency of sparring activity were found. It is unlikely that territoriality existed among the elk studied.

7. Diurnal and "seasonal" variations were found in the frequency with which harem bulls herded cows and calves.

8. 94 % of the heterosexual encounters involved bulls older than 3¹/₂ years. The frequency of heterosexual activity varied diurnally, and "seasonally."

9. Harem bulls chased bulls older than 3¹/₂ years most frequently, spikes less frequently, and 2¹/₂ year old bulls least frequently. In non-contact agonistic encounters the aggressor was always the same age or older than the

aggressee. The frequency of non-contact agonistic encounters varied with the time of day.

10. Sonagrams of alarm barks are presented. The alarm barks of bull elk were of a higher pitch than those of cow elk.

11. The movements of a cow group were, apparently, determined by adult cow(s) and not by bulls or spikes.

12. Bulls older than $3^1/_2$ years spent less time feeding than other age-sex classes. These same bulls spent more time walking and engaged in other activities than did the other classes. It is suggested that bulls older than $3^1/_2$ years develop a negative energy balance during the rut.

Zusammenfassung

Während zweier Monate (1965) wurden im Banff National Park (Kanada) qualitative und quantitative Daten über das Brunftverhalten des amerikanischen Wapiti *(Cervus canadensis)* gesammelt. Einige Verhaltensweisen sind erstmals genauer beschrieben.

Die ♀♀-Gruppen sowie die Zahl der mit ihnen lebenden Spießer und $2^1/_2$- und $3^1/_2$jährigen ♂♂ wurden zu Beginn der Brunft kleiner, an ihrem Ende wieder größer. Das Zahlenverhältnis von ♀♀ und Kälbern blieb dabei gleich. Spießer blieben länger als ältere ♂♂ in den ♀♀-Gruppen und schlossen sich ihnen früher wieder an. Bei Brunftbeginn traten die über $3^1/_2$jährigen ♂♂ zu den ♀♀-Gruppen, spalteten sie und vertrieben jüngere ♂♂.

Sonogramme erläutern genauere Angaben über das Röhren und den Alarmruf, der bei ♂♂ höher ist als bei ♀♀.

Durch Röhren, Geweihschlagen am Gesträuch, Graben und Suhlen scheinen andere ♂♂ aufmerksam und angelockt zu werden. Das führt zu Zweikämpfen und fördert die geschlechtliche Auslese.

♂♂ ab $3^1/_2$ Jahren können ejakulieren beim Röhren, Geweihschlagen, Graben, Stehen in der Suhle, nach dem Zusammentreiben von ♀♀ und beim Alarmrufen.

Heftige Kämpfe waren selten, nur einmal kam es zu Schlägen auf den Körper. Kampfwunden scheinen unwesentlich als Todesursache. ♂♂ kämpfen bevorzugt mit Altersgenossen, ältere kämpfen mehr als junge, alle zu bestimmten Tages- und Jahreszeiten mehr als sonst. Reviere scheint es nicht zu geben.

Harem-♂♂ treiben zu bestimmten Tages- und Jahreszeiten besonders häufig ♀♀ mit Kälbern zusammen. Mehr als $3^1/_2$ Jahre alte ♂♂ bestritten 94 $^0/_0$ der heterosexuellen Kontakte, die ebenfalls tages- und jahreszeitlich verschieden häufig waren.

Harem-♂♂ vertrieben am häufigsten über $3^1/_2$jährige ♂♂, selten Spießer, am seltensten $2^1/_2$jährige ♂♂. Wenn es beim Drohen blieb, war immer der Angreifer gleich alt oder älter als sein Gegner; die Häufigkeit solcher nicht zur Berührung führenden aggressiven Begegnungen änderte sich mit der Tageszeit.

♀♀-Gruppen werden offenbar von adulten ♀♀, nicht von jungen ♂♂ „geführt". Über $3^1/_2$jährige ♂♂ verbrauchen wohl in der Brunft Energiereserven, denn sie fressen weniger lange und sind mehr mit Laufen und anderen Bewegungen beschäftigt als jüngere ♂♂.

Literature cited

ALTMANN, M. (1952): Social behavior of elk, *Cervus canadensis nelsoni,* in the Jackson Hole Area of Wyoming. Behaviour **4,** 116—143 • ALTMANN, M. (1956): Patterns of social behavior in free-ranging elk of Wyoming. Zoologica **41,** 65—71 • ALTMANN, M. (1960): The role of juvenile elk and moose in the social dynamics of their species. Zoologica **45,** 35—39 • BURCKHARDT, D. (1958): Observations sur la vie sociale du cerf *(Cervus elaphus)* au Parc National Suisse. Mammalia **22** (2) • COWAN, I. MCTAGGART and V. GEIST (1961): Aggressive behaviour in deer of the genus *Odocoileus.* J. Mammal **42,** 522—526 • ESPMARK, Y. (1964): Rutting behaviour in reindeer *(Rangifer tarandus* L.). Anim. Behav. **12** (1), 159—163 • ESPMARK, Y. (1964): Studies in dominance-subordination relationship in a group of semi-domestic reindeer *(Rangifer tarandus* L.). Anim. Behav. **12** (4), 420—425 • GEIST, V. (1963): On the behaviour of the North American moose *(Alces alces andersoni* Peterson 1950) in British Columbia. Behaviour **20,** 377—416 • GRAF, W. (1955): The Roosevelt elk. Port Angeles Evening News, Port Angeles, Washington • GRAF, W. (1956): Territorialism in deer. J. Mammal. **37,** 165—170 • HOCKETT, C. F. (1960): Logical considerations in the study of animal communication. In: Animal Sounds and Communication (W. E. LANYON and W. N. TAVOLGA eds.) Washington, D. C.: American Institute of Biological Sciences, 392—430 • LENT, P. C. (1965): Rutting behaviour in a barren-ground caribou population. Anim. Behav. **12** (2—3), 239—264 • MEYER-HOLZAPFEL, M. (1956): Play among the mammals. Translated from Handbuch der Zoologie **8** (10), eds. J. G. HELMCKE and H. V. LENGERKEN • MURIE, O. J. (1932): Elk calls. J. Mammal. **13,** 331—336 • MURIE, O. J. (1951): The elk of North America. Stackpole, Harrisburg, Pennsylvania • PITELKA, F. A. (1959): Numbers, breeding schedule, and territoriality in pectoral sandpipers of northern Alaska. Condor **61** (4), 233—264 • PRUITT, W. O. Jr. (1954): Rutting behavior of the whitetail deer *(Odocoileus virginianus).* J. Mammal. **35** (1), 129—130 • PRUITT, W. O. Jr. (1960): Behavior of the barren-ground caribou. Biological Papers of the University of Alaska No. 3, April, 1960 • SCHNEIDER, K. M. (1930): Das Flehmen. Zool. Garten **3,** 183—198; **4,** 349—364; **5,** 200—226, 287—297 • TURNER, C. D. (1959): General endocrinology. W. B. Saunders Company, Philadelphia, Pennsylvania • YOUNG, V. A. and W. L. ROBINETTE (1939): A study of the range habits of elk on the Selway Game Preserve. Univ. Idaho Bull. **34** (16), 1—48.

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